Simulating forest productivity along a neotropical elevational transect: temperature variation and carbon use efficiency

TOBY R. MARTHEWS*, YADVINDER MALHI*, CÉCILE A. J. GIRARDIN*, JAVIER E. SILVA ESPEJO†, LUIZ E. O. C. ARAGÃO‡, DANIEL B. METCALFE§, JOSHUA M. RAPP¶, LINA M. MERCADO‡,‖, ROSIE A. FISHER**, DAVID R. GALBRAITH*, JOSHUA B. FISHER††, NORMA SALINAS-REVILLA*†, ANDREW D. FRIEND‡‡, NATALIA RESTREPO-COUPE§§ and RICHARD J. WILLIAMS¶¶

*Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, OX1 3QY, UK, †Universidad Nacional de San Antonio Abad del Cusco, Apartado Postal, N° 921, Cusco Perú, ‡College of Life and Environmental Sciences, University of Exeter, Exeter, EX4 4RJ, UK, §Sveriges Lantbruksuniversitet, Skogsmarksgränd, Umeå, 901-83, Sweden, ¶Biology Department, Wake Forest University, Winston-Salem, NC 27109, USA, ‖Centre for Ecology and Hydrology, Wallingford, Oxfordshire, OX10 8BB, UK, **Earth and Environmental Sciences Division, Los Alamos National Laboratory, Los Alamos, NM 87545, USA, ††Jet Propulsion Laboratory, California Institute of Technology, Pasadena, CA 91109, USA, ‡‡Department of Geography, University of Cambridge, Cambridge, CB2 3EN, UK, §§University of Technology Sydney, PO Box 123, Broadway, NSW 2007 Australia, ¶¶Computational Ecology and Environmental Science Group, Microsoft Research, Cambridge, CB3 0FB, UK

Abstract

A better understanding of the mechanisms controlling the magnitude and sign of carbon components in tropical forest ecosystems is important for reliable estimation of this important regional component of the global carbon cycle. We used the *JULES* vegetation model to simulate all components of the carbon balance at six sites along an Andes-Amazon transect across Peru and Brazil and compared the results to published field measurements. In the upper montane zone the model predicted a lack of forest vegetation, indicating a need for better parameterization of the responses of cloud forest vegetation within the model. In the lower montane and lowland zones simulated ecosystem productivity and respiration were predicted with reasonable accuracy, although not always within the error bounds of the observations. Model-predicted carbon use efficiency in this transect surprisingly did not increase with elevation, but remained close to the 'temperate' value 0.5. Upper montane forests were predicted to allocate ~50% of carbon fixation to biomass maintenance and growth, despite available measurements showing that they only allocate ~33%. This may be explained by elevational changes in the balance between growth and maintenance respiration within the forest canopy, as controlled by both temperature- and pressure-mediated processes, which is not yet well represented in current vegetation models.

Keywords: tropical forest production, *JULES* model, field measurements, maintenance respiration, Peru, Brazil

Introduction

Intact tropical forests currently cover 13.9 million km^2 worldwide, or 24% of tropical land area (Pan *et al.*, 2011). These forests support the most biodiverse terrestrial ecosystems in existence (Ghazoul & Sheil, 2010) and provide a basic livelihood for many millions of people (Intergovernmental Panel on Climate Change, 2007), so their importance cannot be overemphasized. Also very significantly, they absorb 1.02 billion tonnes of carbon (Mg C) from the atmosphere every year, approximately 25% of global forest uptake (Malhi,

Correspondence: Toby R. Marthews, tel. + 44 1865 285182, e-mail: Toby.Marthews@ouce.ox.ac.uk

2010; Pan *et al.*, 2011), and in so doing they reduce the rate of global warming by 15% (Malhi, 2010, 2012), making their conservation a crucial element of current policies concerning climate change (Intergovernmental Panel on Climate Change, 2007; Ghazoul & Sheil, 2010).

We need a mechanistic understanding of the components of the tropical forest carbon cycle or 'budget' to translate carbon balance into future forest cover gains and losses under committed climate change (Malhi *et al.*, 1999; Intergovernmental Panel on Climate Change, 2007). Quantifying the carbon budget in terms of standard fluxes in (photosynthesis/productivity) and out (respiration) reveals how global atmospheric carbon dioxide (CO_2) levels are affected by forested areas and *vice versa* (Chambers *et al.*, 2004; Clark, 2004;

Malhi *et al.*, 2009; Malhi, 2010). In addition, ecosystem health, resilience and productivity are increasingly being measured in terms of carbon budgets and carbon gain (Intergovernmental Panel on Climate Change, 2007; Zhang *et al.*, 2009). However, until recently field data on forest biomass stocks and changes did not exist from enough tropical areas either to assess carbon budgets or to constrain modelling efforts adequately for a robust estimation (Marthews *et al.*, 2012). This has resulted in much debate over whether or not tropical forests are a net source or sink of carbon (Chambers *et al.*, 2001, 2004; Clark, 2004; Luyssaert *et al.*, 2008; Lewis *et al.*, 2009; Houghton *et al.*, 2009).

With the advent of large-scale ecosystem research efforts and regional-scale census networks such as the Large Scale Biosphere-Atmosphere Experiment in Amazonia (LBA, Avissar & Nobre, 2002; http://lba. inpa.gov.br/lba/), the Amazon Forest Inventory Network (*RAINFOR*, Malhi *et al.*, 2002; Phillips *et al.*, 2009; http://www.geog.leeds.ac.uk/projects/rainfor/) and the Andes Biodiversity and Ecosystem Research Group (*ABERG*, Malhi *et al.*, 2010; http://darwin.winston.wfu. edu/andes/), data are increasingly becoming available that allow us to assess carbon budgets component by component (Malhi *et al.*, 2009, 2011, Mercado *et al.*, 2011). Tropical ecosystems vary greatly in their spatial and temporal dynamics (Aragão *et al.*, 2009; Zhang *et al.*, 2009; Girardin *et al.*, 2010; Metcalfe *et al.*, 2010; Ghazoul & Sheil, 2010) and accurate and precise quantification of tropical carbon cycling is logistically and physically challenging work (Chambers *et al.*, 2004; Malhi *et al.*, 2009; Metcalfe *et al.*, 2009; Girardin *et al.*, 2010) so uncertainties in individual fluxes remain high. However, measurement methods are improving and the details of the tropical carbon cycle are finding themselves on an ever-firmer scientific basis.

Advances in vegetation models since the mid-1990s, notably the development of Dynamic Global Vegetation Models (DGVMs), have greatly improved the model representation of dynamic canopies and forest biogeochemical cycling (Prentice *et al.*, 2007; Landsberg & Sands, 2011). DGVMs are sophisticated simulators of vegetation dynamics, making use of process-based algorithms and a wide variety of parameters and forcing variables (e.g. Clark *et al.*, 2011; Best *et al.*, 2011). However, the current generation of DGVMs remains relatively poorly verified and validated in tropical climates (Alton *et al.*, 2007; Prentice *et al.*, 2007; Malhi *et al.*, 2011; van de Weg *et al.*, 2012b), despite recent improvements in this direction (e.g. Mercado *et al.*, 2007, 2011). Across the Amazon basin and eastern Andes escarpment, for example, there are strong gradients in temperature, precipitation and seasonality (Phillips *et al.*, 2009; Malhi *et al.*, 2010) and the forests of the region are extremely

diverse not only floristically and structurally (Terborgh & Andresen, 1998; ter Steege *et al.*, 2003; Butt *et al.*, 2008; van de Weg *et al.*, 2009), but also topographically (Grubb & Whitmore, 1966; Ashton, 2003; Malhi *et al.*, 2010), pedologically and hydrologically (Pires & Prance, 1985; Bruijnzeel & Proctor, 1995) and edaphically (Quesada, 2008; Quesada *et al.*, 2010). Despite their sophistication, applying DGVMs in a tropical context is necessarily approximate, but nevertheless these kind of model predictions provide the best available benchmark against which to compare field measurements. Such model-data comparisons are a means of identifying not only quantities that need to be measured more accurately but also processes that need to be represented more reliably in models (van de Weg *et al.*, 2012b).

In this study we focus on the standard carbon fluxes describing productivity and respiration (Table 2). We have also used Carbon Use Efficiency (*CUE*), defined as the ratio of net carbon gain (Net Primary Productivity, *NPP*) to gross carbon assimilation (Gross Primary Productivity, *GPP*), which is a quantity that has received much recent attention (e.g. Malhi *et al.*, 2009). Historically, *CUE* close to 0.50 (i.e. $NPP = GPP/2$) was a common rule-of-thumb in use in temperate forests (Chambers *et al.*, 2004), however, *CUE* is now assumed to vary generally with disturbance and succession (Mäkelä & Valentine, 2001; Yang *et al.*, 2011; e.g. Landsberg & Sands, 2011 suggested that efficiency should decline from $CUE \approx 0.5$ in young forests to $CUE \approx 0.3$ in forests >60 years since disturbance). In the tropics, *CUE* appears to be generally lower than in temperate forests, e.g. Kira (1978) found *CUE* to be 0.35 in Pasoh, Malaysia, Chambers *et al.*, (2004) found 0.32 in old-growth Amazon forests and recent work has found a similar value of 0.30–0.40 across the Amazon and the Andes (Malhi *et al.*, 2009, 2011; Metcalfe *et al.*, 2010; Malhi, 2012). This temperate-tropical difference is clearly visible in maps of worldwide mean annual *CUE* (e.g. Zhang *et al.*, 2009), but the mechanisms behind it remain obscure.

We applied a global vegetation simulator (the Joint UK Land Environment Simulator DGVM, *JULES*; Best *et al.*, 2011; Clark *et al.*, 2011) at six tropical forest sites along an Andes-Amazon elevational gradient in South America (Malhi *et al.*, 2010). Estimates of annual means of the major carbon fluxes were assembled from current LBA, ABERG and RAINFOR projects and used for model validation (for all field protocols followed, see http://gem.tropicalforests.ox.ac.uk/). Finally, feeding back, we carried out additional simulations varying certain model parameters to investigate some avenues for the future development of *JULES*.

The elevation transect provides a unique opportunity to test the ability of vegetation models to capture the

important effects of variation in temperature on ecosystem carbon dynamics (Raich *et al.*, 2006). The transect data themselves are the focus of published or parallel papers (Girardin *et al.*, 2010; Robertson *et al.*, 2010; Farfan Amezquita *et al.*, 2012; Huaraca Huasco *et al.*, 2012; Silva Espejo *et al.*, 2012). In this study we focus on model ability to capture variations in carbon cycling along the transect. We address three research questions: (i) How do simulated forest ecosystem carbon fluxes vary between forests in this Andes-Amazon transect, and how do these fluxes compare with observations? (ii) What are the mechanisms in the model that drive variation in carbon flux components across these sites? and (iii) Is there a net trend of *CUE* with elevation across these sites? Finally, from a consideration of the factors controlling the magnitudes of these carbon flux components, we suggest modifications to some parameters within the *JULES* model that might improve its performance in future tropical studies and, therefore, in future global simulations of the carbon cycle.

Materials and methods

We sampled a tropical elevational transect in the South American Andes (Malhi *et al.*, 2010), extending out into the lowland Amazon basin, by selecting six sites for model simulation (Fig. 1, Table 1). Meteorological data at all six sites were gap-filled where required to produce model-ready driving data sets (Appendix S1). The forest carbon cycle was simulated at all sites using the *JULES* DGVM version 2.2 (released November 2010; Best *et al.*, 2011; Clark *et al.*, 2011, http://www.jchmr.org/jules/) which simulates vegetation productivity from meteorological and forest biometric inputs. For all sites and runs, vegetation cover in *JULES* was fixed at 100% broadleaf with 0% needleleaf (all native tree species in Peru are angiosperms except three uncommon podocarp genera, Pennington *et al.*, 2004, and gymnosperms form a similarly negligible component of the Brazilian Amazon forest, http://floradobrasil.jbrj.gov.br/ so there are no native needleleaf species in any Andes-Amazon biome).

A 650 year spin-up sequence was followed for each simulation, comprising 500 years at pre-industrial levels of atmospheric CO_2 concentration (taken as 285.2 ppmv CO_2 for 1850, Intergovernmental Panel on Climate Change, 2007) followed by a ca. 150 year period of increasing atmospheric CO_2 (slightly longer depending on the starting date of each simulation, see Appendix S1) using global historical values (Intergovernmental Panel on Climate Change, 2007). Because of a lack of reliable time series data, local deviations of Andes-Amazon atmospheric CO_2 levels from global 'well-mixed' values (Park *et al.*, 2007; Pan *et al.*, 2011), seasonal cycles in CO_2 concentration (Park *et al.*, 2007) and sub-daily cycles (Walsh, 1996; Iwata *et al.*, 2005) were not simulated. The vegetation dynamics module (TRIFFID) was activated to allow vegetation carbon pools to be updated but not fractional cover.
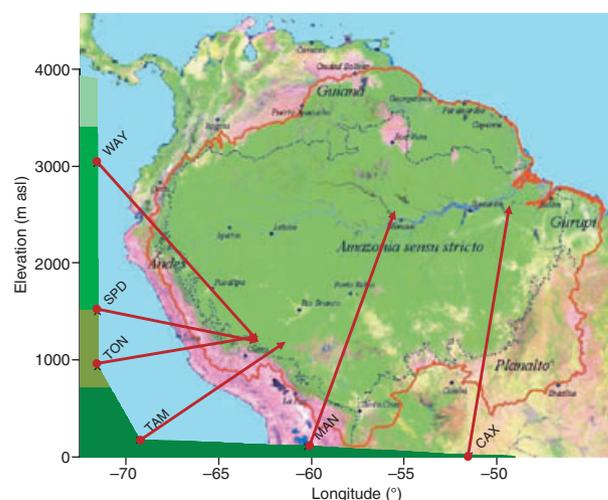

Fig. 1 The six study sites and a vertical profile of the Andes-Amazon transition in relation to Amazonia as defined in Eva *et al.*, (2005). On the map, the broken black outline shows Amazonia sensu stricto (the Amazon basin below 700 m asl, Eva *et al.*, 2005). On the graph, shading represents Puna grassland above the treeline at approximately 3400 m asl (Girardin *et al.*, 2010), upper montane forest above the consistent cloud base at approximately 1500 m asl (Ashton, 2003), lower montane forest and the lowlands in Amazonia sensu stricto. All sites are part of the *RAINFOR* network (Malhi *et al.*, 2002) and the nearby flux towers at Manaus and Caxiuanã are part of the LBA experiment (Avissar & Nobre, 2002). Base map used with permission from the Joint Research Centre, Institute for Environment and Sustainability, © European Communities, 2005.

Default *JULES* photosynthetic parameters (Clark *et al.*, 2011) were used for all runs apart from the parameters controlling the nitrogen (N) concentration of top-of-canopy leaves in simulated broadleaf trees (N_{l0}) and photosynthetic capacity (V_{Cmax25}) for which more accurate local values were available (Table 1; note that the constant of proportionality $n_e = V_{Cmax25}/N_{l0}$ was altered from its default value 0.0008 mol CO_2 m^{-2} s gC/gN for C$_3$ vegetation to accommodate this, see Clark *et al.*, 2011). Note that, although leaf N concentration was assumed constant down the canopy in previous versions of *JULES* (up to v2.0), the leaf-canopy scale-up option # 4 of v2.2 incorporates the work of Mercado *et al.*, (2006, 2007) which specifies a leaf N profile exponentially decreasing from N_{l0} to lower values in the understorey (notably with an exponent different from that describing the decrease in radiation: see Lloyd *et al.*, 2010).

The *JULES* assumes that canopy height h (in m) and *LAI* at equilibrium are allometrically related as $LAI_{eq} = (\eta_{sl}a_{ws}h_{eq}/a_{wl})^{\frac{3}{2}}$ where η_{sl} is a live stemwood coefficient (default value = 0.01 kg C m^{-2} per unit *LAI* for broadleaf trees), a_{ws} is the ratio of total to respiring stem carbon (= 10 for woody plants) and a_{wl} is an allometric coefficient relating woody biomass to *LAI* (=0.65 kg C m^{-2} for trees) (Clark *et al.*, 2011). Therefore, measured values for canopy height and *LAI* were accommodated by specifying appropriate values for the η_{sl} parameter from $\eta_{sl} = a_{wl}LAI_{eq}^{2/3}/a_{ws}h_{eq}$ (Table 1).

Table 1 Characteristics of the six study sites. Values for V_{Cmax25}, the photosynthetic capacity (maximum rate of RuBisCO carboxylation) at 25 °C, were taken from van de Weg *et al.* (2012), applying their lowland (Manaus) value to all sites up to San Pedro because of their broadly similar values for Nl0. For reference, the *JULES* default values for broad-leaf vegetation are $N_{l0} = 0.046$ g N / g C and $V_{Cmax25} = 36.8$ mol CO_2/m^2s, so the constant of proportionality ne = $VC_{max25}/N_{l0} = 0.0008$ mol $CO_2/m^2s \bullet$ g C / g N (a measure of photosynthetic nitrogen use efficiency, Cox 2001; Clark *et al.* 2011).

Plot	Location			Biome	Elevation above sea level (m)	Mean annual temperature (°C)	Annual precipitation (mm)
Wayqecha	Intensive census plot WAY-01 (WA_3000) at the Estación Biológica Wayqecha	Cusco, Peru	13° 11' 25.45" S 71° 35' 13.56" W	Cloud forest / upper montane forest	3025	12.5	1706
San Pedro plot 2	Census plot SPD-02 (SP_1500) in the Kosñipata transect	Cusco, Peru	13° 2' 56.89" S 71° 32' 12.64" W	Upper/lower montane transition zone	1500	18.8	2631
Tono plot 1	Census plot TON-01 (TO_1000) in the Kosñipata transect	Cusco, Peru	12° 57' 16.92" S 71° 33' 12.75" W	Lower montane forest	925	20.7	3087
Tambopata plot 4	Intensive census plot TAM-06 (Tambopata plot 4) at the Centro de Investigaciones Tambopata	Madre de Dios, Peru	12° 50' 18.59" S 69° 17' 45.65" W	Lowland terra firme forest	200	26.4	2730
Manaus, K34 Tower	A mean of census plots MAN-01 and MAN-02 close to the LBA K34 eddy covariance flux tower	Amazonas, Brazil	2° 35' 21.08" S 60° 6' 53.63" W	Lowland terra firme forest	104	27.3	2250
Caxiuanã Tower plot	Intensive census plot CAX-06 at the Estação Científica Ferreira Penna	Pará, Brazil	1° 43' 11.26" S 51° 27' 29.45" W	Lowland terra firme forest	12	26.9	2314

Table 1 (continued)

Plot	Canopy height (h, m)	Leaf Area Index (LAI, m²/m²)	Live stemwood coefficient η_{sl} (kg C/m² per unit LAI)	Soil texture (% clay, % sand)	Canopy top-leaf N:C ratio N_{l0} (g N/g C)	Maximum rate of carboxylation of RuBisCO at 25°C V_{cmax25} (μmol CO₂/m²s)	$n_e = V_{cmax25}/N_{l0}$ (mol CO₂/ m²s · g C/g N)
Wayqecha	14 ††††¶¶¶¶	4 ††††	0.012	16%, 12% ‡‡‡	0.024 ‡‡‡‡¶¶¶¶	55.6 §§§§§	0.00232
San Pedro plot 2	18.5 ††††¶¶¶¶	5 †††††	0.010	16%, 13% ‡‡‡	0.054 ‡‡‡‡,******	42.8 §§§§§	0.00079
Tono plot 1	29 ††††¶¶¶¶	5 †††††	0.007	5%, 64% ‡‡‡	0.050 ‡‡‡‡,††††††	42.8 §§§§§	0.00086
Tambopata plot 4	30 §§	5 ****	0.006	7%, 66% ‡‡‡	0.051 (=24.80/485) **	42.8 §§§§§	0.00084
Manaus, K34 Tower	30 ***	5.58 *****	0.007	68%, 20% ¶	0.045 (=22.33/491 from the nearby Jacaranda site) **	42.8 §§§§§	0.00095
Caxiuanã Tower plot	35 ††††,§§	5.25 *****	0.006	44%, 38% *****	0.042 (=19.80/468) **	42.8 §§§§§	0.00102

*Lisboa (1997),
†Araújo et al., (2002),
‡Amorim Costa (2005),
§Iwata et al., (2005),
¶Quesada (2008),
**Fyllas et al., (2009),
††Patiño et al., (2009),
‡‡Shuttle Radar Topography Mission (SRTM) elevations from Anderson et al., (2009) with canopy height subtracted,
§§Aragão et al., (2009),
¶¶Malhi et al., (2009),
***Mercado et al., (2009),
†††van de Weg et al., (2009),
‡‡‡Zimmermann et al., (2009a, b Zimmermann et al., 2010,
§§§A. C. Araújo pers. comm. to N. Restrepo-Coupe July 2009,
¶¶¶Girardin et al., (2010),
****Metcalfe et al., (2010),
††††Robertson et al., (2010),
‡‡‡‡Salinas et al., (2011).
§§§§Global Positioning System (GPS) reading taken by J. Rapp,
¶¶¶¶Maximum measured tree height, J. Fisher and I. Torres (unpubl. data),
*****Patiño et al., (unpubl. data),
†††††Estimated for this study (Wayqecha value is close to the 4.17 m²/m² in van de Weg et al., 2012b),
‡‡‡‡‡N. Salinas (unpubl. data),
§§§§§van de Weg et al., (2012a),
¶¶¶¶¶Mean of sun leaves sampled from Clusia cretosa, Hesperomeles ferruginea and Weinmannia crassifolia trees, the commonest species in this plot,
******Mean of sun leaves sampled from Vismia sp., Alchornea latifolia and Tachigali sp. trees, the commonest species in this plot,
††††††Mean of sun leaves sampled from Symphonia globulifera, Perebea guianensis and Virola elongata trees, the commonest species in this plot.

Soil layers 0–10, 10–35, 35–100 cm and 1–4 m were simulated with the van Genuchten soil hydrology option (Hodnett & Tomasella, 2002; Marthews *et al.*, 2008; Best *et al.*, 2011). The standard pedotransfer functions of Cosby *et al.*, (1984) were applied to measured soil textures (Table 1) to calculate the parameters of the soil water characteristic, under the assumption that the van Genuchten model parameters may be approximated by Clapp & Hornberger model parameters (see Dharssi *et al.*, 2009).

The Joint UK Land Environment Simulator, *JULES* was run at each study site under several parameter combinations in a full factorial design: (i) with the live stemwood coefficient η_{sl} set at the site-specific value (required to balance known canopy height and *LAI*) and at the default value (Table 1), (ii) with the canopy top-leaf N : C ratio N_{l0} set at the site-specific value and at the value corresponding to the Caxiuanã site (Table 1), (iii) with the proportion of *GPP* allocated to growth r_g set at $r_g = 0.15$, $r_g = 0.25$ (default value) and $r_g = 0.35$ (see Appendix S2 for definition and explanation of this quantity), (iv) with the Plant Functional Type (PFT) parameters controlling the upper and lower bounds of photosynthesis set to default broadleaf values $T_{low} = 0$ °C, $T_{upp} = 36$ °C and default needleleaf values $T_{low} = -10$ °C, $T_{upp} = 26$ °C (see Clark *et al.*, 2011) to test PFT-specific effects (despite the lack of native needleleafs, this tests whether or not the (broadleaf) cloud forest vegetation behaves as if it has needleleaf temperature tolerances), (v) with the correct meteorological driving data set for the site (as described Appendix S1) and with the driving data replaced with the data from Caxiuanã to test meteorology-specific effects. All analyses were done using R version 2.13.1 (R Development Core Team, 2011).

Results

With fractional cover held at 100% broadleaf, *JULES* predicted *LAI* to decrease to 0.1 m^2 m^{-2} (i.e. disappearance of almost all vegetation) at Wayqecha, the highest elevation site (3025 m asl), when all other sites supported *LAI* at 4.5–5.0 m^2 m^{-2}. This had the effect of reducing all fluxes to minimal (but nonzero) values but *JULES* nevertheless did return a reasonable prediction of *CUE*. This reduction to minimal cover at altitude happened under all parameter combinations (even if the temperature limits for photosynthesis were changed to default needleleaf values) except when the Caxiuanã (lowland) meteorology was used. The minimal vegetation simulated at Wayqecha should be borne in mind when interpreting the following results concerning bulk carbon quantities (see Table 2 for definitions):

Gross primary productivity (*GPP*). *JULES*'s predictions for overall mean *GPP* were broadly constant with temperature in the lowlands, lying towards the top of the Luyssaert *et al.*, (2007) band, slightly underestimating *GPP* at Manaus in comparison with measurements

(Fig. 2a). *JULES* predicted declining *GPP* with decreasing temperature (i.e. with increasing elevation) in the upper and lower montane zones, but declining faster than measurements would suggest (Fig. 2a). With Caxiuanã (lowland Brazilian Amazon) meteorology imposed, simulated *GPP* rose to Caxiuanã levels at all sites confirming that simulated *GPP* is highly sensitive to meteorological conditions in the model. Changing η_{sl}, N_{l0} or r_g did not affect *GPP*, but changing T_{low} and T_{upp} to needleleaf values had the effect of capping mean *GPP* to approximately 20 Mg C ha^{-1} yr^{-1} at all sites.

Autotrophic respiration (R_a). *JULES*'s predictions for overall mean R_a were within observation error at Manaus and Caxiuanã, but otherwise lower than both measurements and what the Luyssaert *et al.*, (2007) band would suggest (Fig. 2b). *JULES* predicted declining R_a with decreasing temperature along the whole transect (Fig. 2b). With Caxiuanã meteorology imposed, R_a rose to Caxiuanã levels at all sites confirming that simulated R_a is highly sensitive to meteorological conditions in the model. Changing η_{sl} or N_{l0} did not affect R_a, but changing T_{low} and T_{upp} to needleleaf values had the effect of capping mean R_a to approximately 10 Mg C ha^{-1} yr^{-1} at all sites. Increasing r_g by 0.10 had the effect of increasing R_a by approximately 11.4% at all sites (and decreasing r_g by 0.10 decreased R_a by the same amount).

Heterotrophic respiration (R_h). In most of the lower montane and lowland zones, *JULES*'s predictions for overall mean R_h were higher than both measurements and what the Luyssaert *et al.*, (2007) band would suggest (Fig. 2c). *JULES* predicted declining R_h with decreasing temperature only in the montane zones, but again with too steep a decline in the upper montane zone (Fig. 2c). With Caxiuanã meteorology imposed, R_h rose to Caxiuanã levels at all sites confirming that simulated R_h is highly sensitive to meteorological conditions in the model. Changing η_{sl} or N_{l0} did not affect R_h, but changing T_{low} and T_{upp} to needleleaf values had the effect of capping mean R_h to approximately 10 Mg C ha^{-1} yr^{-1} at all sites. Increasing r_g by 0.10 had the effect of decreasing R_h by approximately 13.6% at all sites (and decreasing r_g by 0.10 increased R_h by the same amount).

Net primary productivity (Total *NPP*, the sum of above- and below-ground *NPP*). Apart from San Pedro, Manaus and the measurements of Aragão *et al.*, (2009) at Tambopata, in the lower montane and lowland zones *JULES*'s predictions for overall mean *NPP* were higher than both measurements and what the Luyssaert *et al.*, (2007) band and Clark *et al.*, (2001b) would suggest, although still lower than the assumptions of the precipitation-based *MIAMI* model (Fig. 2d). *JULES* predicted

Table 2 Measured forest carbon fluxes (definitions follow Intergovernmental Panel on Climate Change, 2007, e.g. http://www.ipcc.ch/publications_and_data/publications_and_data_glossary.shtml). Sites used for *JULES* simulation runs in this study are in bold (Table 1) and some nearby sites where data are available are included for reference. Note that the 'plant respiration' *respP* and 'soil respiration' *respS* in outputs from *JULES* correspond to R_a (= whole plant respiration including root respiration) and R_h (= soil respiration minus root respiration) as defined here (Clark *et al.*, 2011). All confidence intervals are mean ± 1SE except for those from Metcalfe *et al.*, (2010) which are mean ± 95% CI. Note: in this text we calculate Carbon Use Efficiency (*CUE*) at subdaily timesteps, despite this being arguably difficult to interpret because forests are known to store photosynthates for later use over daily periods. A carbon flux of 1 Mg C ha^{-1} yr^{-1} = 100 g C m^{-2} per year and, when considered over sub-daily time periods, = 0.264 μmol C m^{-2} s = 0.264 μmol CO$_2$ m^{-2} s (and when converted to biomass units - i.e. g dry matter rather than g C - these productivities may be thought of as growth rates)

Forest bulk carbon fluxes outside large disturbance events (Mg C ha^{-1} yr^{-1}, where 'bulk' means summed over all plants and soil to make a canopy-averaged, per ha figure)

Plot (code)	Gross Primary Productivity (gross carbon fixation/assimilation; gross photosynthesis less photorespiration) GPP	Autotrophic (plant-derived) Respiration R_a	Heterotrophic (not derived from plants) Respiration R_h (=$R_{eco} - R_a$ where R_{eco} is ecosystem respiration)	Net Primary Productivity (the carbon equivalent of above- and below-ground biomass production; short-term net carbon uptake) NPP (=$GPP - R_a$)	Net Ecosystem Productivity (medium-term net carbon uptake) $NEP^{*,\dagger}$ (=$NPP - R_h = GPP - R_{eco}$)	Carbon Use Efficiency (ratio of net carbon gain to gross carbon assimilation; the fraction of carbon fixed that is allocated to growth; $CUE = NPP/GPP$ $= 1 - (R_a/GPP)$)
Wayqecha (WAY-01)	$25.23 \pm 0.83^{\ddagger}$	$16.97 \pm 0.72^{\ddagger}$	$9.52 \pm 0.23^{\ddagger}$	$8.26 \pm 0.41^{\ddagger}$	$-1.26 \pm 0.47^{\ddagger,\S}$	$0.33 \pm 0.02^{\ddagger}$
Wayqecha Esperanza plot	$21.97 \pm 0.83^{\ddagger}$	$14.78 \pm 0.73^{\ddagger}$	$8.32 \pm 0.45^{\ddagger}$	$7.20 \pm 0.39^{\ddagger}$	$-1.12 \pm 0.60^{\ddagger,\S}$	$0.33 \pm 0.02^{\ddagger}$
Trocha Union plot 3 (TRU-03)			$3.05 \pm 0.47^{\P}$	$4.11 \pm 0.26^{\P}$	$1.06 \pm 0.73^{\P,\S}$	
Trocha Union plot 4 (TRU-04)			$4.31 \pm 0.74^{\P}$	$5.98 \pm 0.39^{\P}$	$1.67 \pm 1.13^{\P,\S}$	
Trocha Union plot 7 (TRU-07)			$3.66 \pm 0.38^{\P}$	$4.50 \pm 0.20^{\P}$	$0.84 \pm 0.58^{\P,\S}$	
Trocha Union plot 8 (TRU-08)			$5.14 \pm 0.80^{\P}$	$5.97 \pm 0.73^{\P}$	$0.83 \pm 1.53^{\P,\S}$	
San Pedro plot 1 (SPD-01)	$30.03 \pm 2.25^{**}$	$22.11 \pm 2.21^{**}$	$9.64 \pm 0.71^{**}$	$7.92 \pm 0.39^{**}$	$-1.72 \pm 0.81^{**,\S}$	$0.26 \pm 0.02^{**}$
San Pedro plot 2 (SPD-02)	$38.31 \pm 2.54^{**}$	$26.39 \pm 2.50^{**}$	$11.59 \pm 0.25^{**}$	$11.92 \pm 0.46^{**}$	$0.33 \pm 0.52^{**,\S}$	$0.31 \pm 0.02^{**}$
Tono plot 1 (TON-01)			$5.64 \pm 2.25^{\P}$	$7.07 \pm 0.98^{\P}$	$1.43 \pm 3.23^{\P,\S}$	
Tambopata plot 3 (TAM-05)	$37.11 \pm 2.50^{\dagger\dagger}$	$23.48 \pm 2.42^{\dagger\dagger}$	$12.07 \pm 0.78^{\dagger\dagger}$	$13.63 \pm 0.65^{\dagger\dagger}$	$1.56 \pm 1.02^{\dagger\dagger,\S}$	$0.37 \pm 0.03^{\dagger\dagger}$
Tambopata plot 4 (TAM-06)	$34.69 \pm 2.53^{\dagger\dagger}$	$22.24 \pm 2.43^{\dagger\dagger}$	$10.64 \pm 0.66^{\dagger\dagger}$	$12.45 \pm 0.71^{\dagger\dagger}$	$1.81 \pm 0.97^{\dagger\dagger,\S}$	$0.36 \pm 0.03^{\dagger\dagger}$
Manaus, K34 Tower	$30.4^{\ddagger\ddagger,\S\S}$	$19.8 \pm 4.6^{\S\S}$	$9.6 \pm 1.2^{\S\S}$	$10.1 \pm 1.4^{\S\S}$, $11.40 \pm 1.29^{\P}$	$0.5 \pm 2.6^{\S\S,\S\S}$	$0.34 \pm 0.10^{\S\S}$

Table 2 (continued)

Forest bulk carbon fluxes outside large disturbance events (Mg C ha^{-1} yr^{-1}, where 'bulk' means summed over all plants and soil to make a canopy-averaged, per ha figure)

Plot (code)	Gross Primary Productivity (gross carbon fixation/ assimilation; gross photosynthesis less photorespiration) GPP	Autotrophic (plant-derived) Respiration R_a	Heterotrophic (not derived from plants) Respiration R_h ($=R_{eco}-R_a$ where R_{eco} is ecosystem respiration)	Net Primary Productivity (the carbon equivalent of above- and below-ground biomass production; short-term net carbon uptake) NPP ($=GPP-R_a$)	Net Ecosystem Productivity (medium-term net carbon uptake) $NEP^{*,\dagger}$ ($=NPP-R_h=GPP-R_{eco}$)	Carbon Use Efficiency (ratio of net carbon gain to gross carbon assimilation; the fraction of carbon fixed that is allocated to growth; $CUE=NPP/GPP$ $=1-(R_a/GPP)$)
Caxiuanã Tower plot (CAX-06)	38.2 ± 2.0 [§§], 33.0 ± 2.9 [***], 32.0 ± 4.1 [†††]	21.4 ± 4.1 [§§], 22.4 ± 2.8 [***], 24.4 ± 4.1 [†††]	9.4 ± 0.8 [§§], 10.2 ± 1.0 [***], 9.9 ± 0.8 [†††]	10.0 ± 1.2 [§§], 10.90 ± 1.11 [¶¶], 10.6 ± 0.9 [***], 10.6 ± 0.7 [†††]	0.6 ± 2.0 [§§], 0.4 ± 1.9 [***], 0.7 ± 1.5 [†††]	0.32 ± 0.07 [§§], 0.32 ± 0.04 [***], 0.33 ± 0.05 [†††]

*Positive NEP means that the carbon pool of the ecosystem is usually expanding, i.e. it is a net carbon sink outside large disturbance events. We avoid the term Net Ecosystem Exchange (NEE) because this is sometimes defined as the net CO_2 flux to the atmosphere (outside large disturbances), which equals -NEP (e.g. Clark *et al.*, 2001a; Malhi *et al.*, 2009; Houghton *et al.* 2009) and sometimes defined to equal NEP (e.g. Chapin *et al.*, 2002; Landsberg & Waring, 2004; Luyssaert *et al.*, 2007; Bonan, 2008).

†There is often confusion between NEP and the related concept of Net Biome Productivity (NBP, which is long-term net carbon uptake ('NEP minus disturbance') i.e. net ecosystem productivity averaged over both normal productivity and large disturbance events, Intergovernmental Panel on Climate Change, 2007): see Malhi *et al.* (1999) and Lovett *et al.* (2006) for discussions.

‡Silva Espejo *et al.* (2012).

§Calculated here from $NPP-R_h$.

¶Girardin *et al.* (2010; n.b. respiration from coarse woody debris was not included in their measurements so they may have underestimated R_h by possibly as much as 50%).

**Huaraca Huasco *et al.* (2012).

††Farfan Amezquita *et al.* (2012).

‡‡Malhi & Grace (2000).

§§Malhi *et al.* (2009).

¶¶Aragão *et al.* (2009).

***Metcalfe *et al.* (2010; taking GPP = plant carbon expenditure PCE which is legitimate for annual fluxes: because of seasonal storage terms, PCE may differ from GPP at sub-annual timescales).
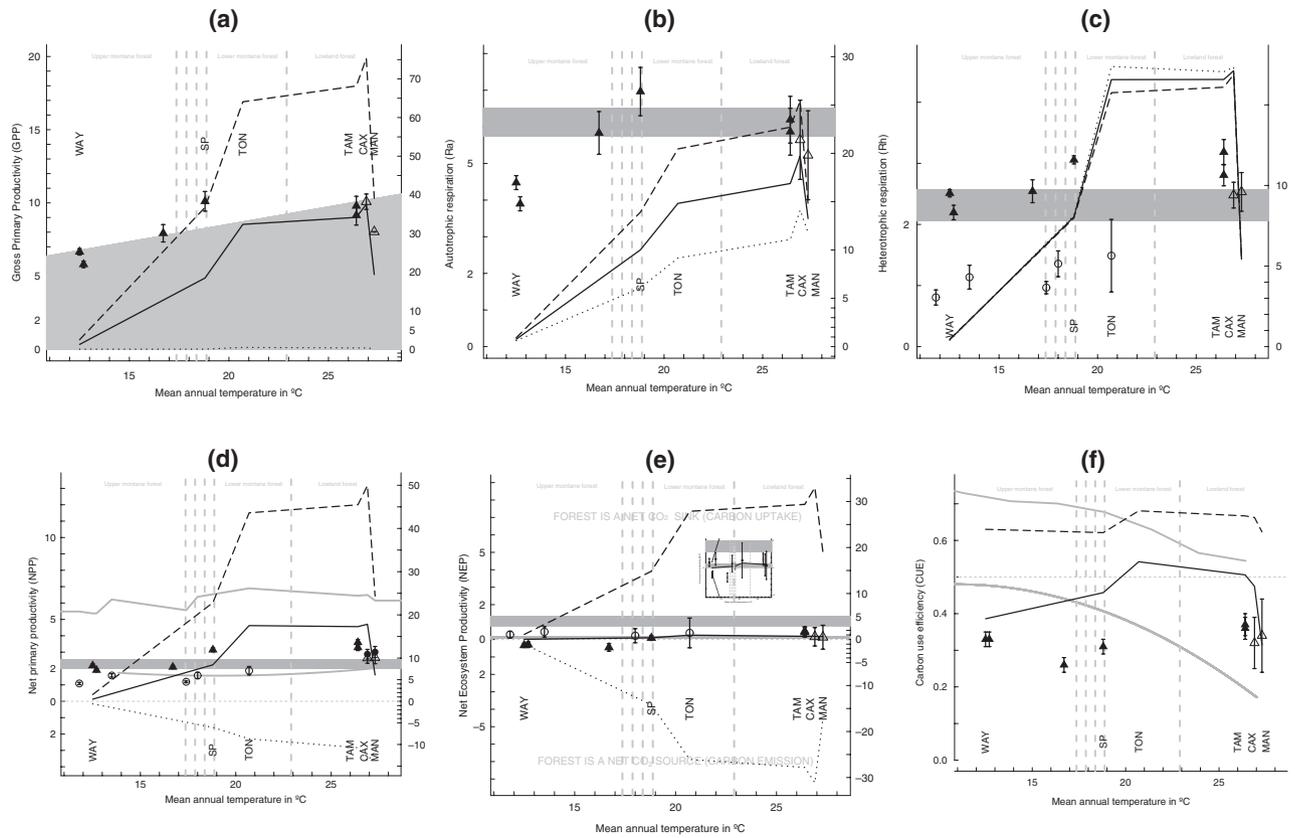
†††Malhi *et al.* (2011).

Fig. 2 Simulated carbon fluxes for all sites plotted against mean annual temperature and compared to field measurements: (a) Gross Primary Productivity (*GPP*), (b) Autotrophic respiration (*R*$_a$), (c) Heterotrophic soil respiration (*R*$_h$), (d) Total Net Primary Productivity (*NPP*), (e) Net Ecosystem Productivity (*NEP*) with an inset expanding the values close to *NEP* = 0 and (f) Carbon Use Efficiency (*CUE*=*NPP/GPP*) as defined in Table 2. Units in plots (a–e) are μmol CO_2 m^{-2} s^{-1} (left vertical axis) or equivalent mean annual flux in Mg C ha^{-1} yr^{-1} (right axis; n.b. 1 Mg C ha^{-1} yr^{-1} = 100 g C m^{-2} per year = 0.264 μmol C m^{-2} per second). *JULES* results are shown as lines: overall means (solid), daylight means (broken) and nighttime means (dotted, undefined in f) to show daily variation at each site. Measurement points are from Farfan Amezquita *et al.*, (2012), Huaraca Huasco *et al.*, (2012), Silva Espejo *et al.*, (2012) (all three follow the same methods; all shown as ▲, ±1SE), Aragão *et al.*, (2009, ●, ±1SE), Malhi *et al.*, (2009, Δ, ± 1SE) and Girardin *et al.*, (2010, ○, ±1SE; n.b. respiration from coarse woody debris was not included in their measurements so they may have underestimated *R*$_h$ by possibly as much as 50%) (q.v. Table 2). Site names (e.g. WAY = Wayqecha) are displayed above/below their corresponding points (sites between Wayqecha and San Pedro (q.v. Table 2) are shown for reference only and were not used in any analysis). Grey bands on (a–d) show the range of values found by Luyssaert *et al.*, (2007) for tropical humid evergreen forests, and also for reference we show: on (d) the average of the 'low' an 'high' *NPP* regressions against temperature found by Clark *et al.*, (2001b) in old-growth tropical forest sites up to 2500 m asl (lower grey curve) and the global *NPP* regression against precipitation used in the *MIAMI* model widely used in the 1970s (Scurlock & Olson, 2002) (upper grey curve); on (e) the pantropical (forest) synthesis of Malhi (2010) (lower grey curve) and the range of values found by Luyssaert *et al.*, (2007) for tropical humid evergreen forests (upper grey curve); on (f) the *CUE* regression against temperature found by Piao *et al.*, (2010) from a global database of eddy covariance and direct field measurements from 60 sites including 4 tropical forests (lower grey curve) and the global *CUE* relationship against altitude proposed by Zhang *et al.*, (2009) (upper grey curve). Also for reference, a $y = 0$ line is shown on all plots except (f) where a *CUE*=0.5 line is shown, and vertical dashed lines show the transition zone at 1500–1800 m asl above which cloud cover is consistent (upper montane forest, Ashton, 2003) and the boundary at 700 m asl below which is lowland forest (Eva *et al.*, 2005). Finally, note that during the night *GPP* = 0 so *CUE* should be undefined, but nevertheless the plotted daylight mean does not coincide with the overall mean line. This is because at timesteps shortly after dusk on many simulated days *JULES* predicts slightly negative *NPP* (caused by nonzero *R*$_a$, perhaps indicating investment in new structures such as buds or leaves or general remobilization of stored carbon, van Oijen *et al.*, 2010) and small but nonzero *GPP* as *GPP* tends to zero (due to lag effects), giving a negative nighttime mean for *CUE*.

declining *NPP* with decreasing temperature only in the montane zones, but again with too steep a decline in the upper montane zone (Fig. 2d). With Caxiuanã

meteorology imposed, *NPP* rose to Caxiuanã levels at all sites confirming that simulated *NPP* is highly sensitive to meteorological conditions in the model.

Changing η_{sl} or N_{l0} did not affect *NPP*, but changing T_{low} and T_{upp} to needleleaf values had the effect of capping mean *NPP* to approximately 10 Mg C ha^{-1} yr^{-1} at all sites. Increasing r_g by 0.10 had the effect of decreasing *NPP* by approximately 13.6% at all sites (and decreasing r_g by 0.10 increased *NPP* by the same amount).

Net ecosystem productivity (*NEP*). In the lower montane and lowland zones *JULES* simulated a small CO_2 sink at all sites broadly in line with the Malhi (2010) band, which agreed with measurements at all lowland and lower montane sites, although these sinks were smaller in magnitude than the suggested Luyssaert *et al.*, (2007) sink (Fig. 2e). *JULES* predicted no consistent trend of *NEP* with elevation or temperature (Fig. 2e). With Caxiuanã meteorology imposed, *NEP* converged to Caxiuanã levels at all sites. Changing η_{sl} or N_{l0} did not affect *NEP*, but changing T_{low} and T_{upp} to needleleaf values had the effect of capping mean *NEP* to approximately 0.6 Mg C ha^{-1} yr^{-1} at all sites. Increasing r_g by 0.10 had the effect of decreasing *NEP* by approximately 11.6% at all sites (and decreasing r_g by 0.10 increased *NEP* by the same amount).

Carbon use efficiency (*CUE*, = *NPP/GPP*). Simulated values for overall mean fitted all measurement values except San Pedro fairly well, though with some overestimation (Fig. 2f). *JULES* predicted no consistent trend of *CUE* with elevation or temperature, notably not confirming the consistent increase with elevation expected from the results of Zhang *et al.*, (2009) or Piao *et al.*, (2010) (Fig. 2f). With Caxiuanã meteorology imposed, *CUE* rose to Caxiuanã levels at all sites. Changing η_{sl} or N_{l0} did not affect *CUE*, but changing T_{low} and T_{upp} to needleleaf values had the effect of reducing mean *CUE* by approximately 0.04 across all sites. Increasing r_g by 0.10 had the effect of decreasing *CUE* by approximately 0.06 at all sites (and decreasing r_g by 0.10 increased *CUE* by the same amount).

In summary, in the upper montane zone *JULES* predicts a lack of forest vegetation. In the lower montane and lowland zones *JULES* overestimates *NPP* and R_a, underestimates R_h but predicts *GPP*, *NEP* and *CUE* fairly well.

Discussion

Forest productivity, respiration and carbon use efficiency are controlled by a variety of factors along our elevational transect, which encompasses several tropical forest biomes and therefore many different species compositions and canopy architectures (see general reviews Friend & Woodward, 1990; Malhi & Grace, 2000; Landsberg & Sands, 2011). Although temperature effects are arguably the most important (Friend &

Woodward, 1990; Raich *et al.*, 2006), as Ashton (2003) pointed out, if the boundaries between biomes along elevational gradients were controlled entirely by temperature then the Massenerhebung effect (e.g. Richards *et al.*, 1996) would require much greater global variation in lapse rates than is observed in reality (also see Zach *et al.*, 2010). We concentrate here on our first two research questions: how do ecosystem carbon budgets vary along our study transect and what are the mechanisms driving this variation?

Gross primary productivity

Within the known limits of the vegetation simulator used, our results for simulated *GPP* were in line both with measurements and with the upper half of the range of values suggested by Luyssaert *et al.*, (2007). Photosynthesis (carbon fixation per unit leaf area) varies with temperature according to the Farquhar – von Caemmerer – Berry model (Cox, 2001; Clark *et al.*, 2011; Landsberg & Sands, 2011) which for these sites, where temperatures are usually below the optimal temperature for photosynthesis (approximately 25 °C, Landsberg & Sands, 2011), means that *GPP* declines with decreasing temperature (as found by Raich *et al.*, 2006; also see van de Weg *et al.*, 2012b). This trend fully supports our *JULES* simulations.

The *GPP* declines with decreasing radiative input (e.g. Zach *et al.*, 2010; van de Weg *et al.*, 2012b; received SW radiation at Wayqecha was 103 W m^{-2} in annual mean compared to 152 W m^{-2} in the lowland sites) and radiation is one of the drivers of seasonality in at least our upper montane sites (Silva Espejo *et al.*, 2012). This trend fully supports our simulations and therefore provides an alternative driver for the decline of *GPP* along our transect. It has also been noted that cloud cover increases the proportion of diffuse radiation and, because diffuse radiation penetrates vegetation canopies more efficiently than direct, this may increase photosynthesis (Graham *et al.*, 2003; Mercado *et al.*, 2007; Marthews *et al.*, 2012), at least in cases where an increase in diffuse radiation is not associated with a decrease in total photosynthetically active radiation *PAR* (van de Weg *et al.*, 2012b).

Despite their high rainfall and moist climate, tropical forests are well known to experience significant dry periods (seasonal as well as short spells) (Richards *et al.*, 1996; Walsh, 1996; Fisher *et al.*, 2008; Marthews *et al.*, 2008; Metcalfe *et al.*, 2010) and water limitation can be a control of *GPP* (at sub-annual timescales also called Plant Carbon Expenditure PCE, Table 2). Surface soil moisture in the transect is approximately equal in the upper montane and lowland zones, and slightly higher in the lower montane zone because of oro-

graphic rainfall at the Andes escarpment (Zimmermann *et al.*, 2010), but there are not yet enough data from mid-elevations to show conclusively how much variability in *GPP* is explained by precipitation. Soil texture and nutrients (Pires & Prance, 1985; Quesada, 2008) are also known to account for some regional variation in carbon fluxes (Friend & Woodward, 1990; Chambers *et al.*, 2004; Malhi *et al.*, 2009; Aragão *et al.*, 2009), but, as is standard for DGVMs, soil types are only accounted for in the parameterization of *JULES* in terms of soil hydraulic properties (see Methods). To account for soil moisture stress on photosynthesis, *JULES* uses a multiplicative soil moisture stress factor (*ß*) in its *GPP* calculations (a fraction 0–1 with higher meaning greater soil water availability; Clark *et al.*, 2011). The value of *ß* during the simulations was consistently high (mean > 0.93 across all simulation time points), indicating almost no water limitation (as found in van de Weg *et al.*, 2012b), except at Manaus, which experienced several dry periods during its simulation periods (mean = 0.53), and possibly Tono (mean = 0.81). Surprisingly, according to current data, soil moisture content does not explain the variability in *GPP* along this transect either in simulations or in the field (Zimmermann *et al.*, 2010).

Gross Primary Productivity, *GPP* is known to increase with the leaf N content of canopy leaves (via leaf RuBisCO content and therefore increased photosynthetic capacity V_{Cmax}, see e.g. Mercado *et al.*, 2007, 2011; Clark *et al.*, 2011 and review in Lloyd *et al.*, 2010). A standard theory to explain lower *GPP* at higher elevations is therefore that montane forests are N-limited ecosystems (Bruijnzeel & Proctor, 1995; Tanner *et al.*, 1998), with reduced *GPP* occurring through direct effects (lower leaf N because of a reduced N mineralization rate) and also indirect effects (e.g. decreased active *LAI* because of constrained leaf production or an altered vertical profile of leaf density in the canopy) (Moser *et al.*, 2011). Leaf measurements, however, show that only Wayqecha has significantly lower foliar N than lowland values in this transect (Table 1, Salinas *et al.*, 2011; Fisher *et al.*, 2011; van de Weg *et al.*, 2012a, 2012b) so N limitation can only be significant in our upper montane zone at most (cf. Moser *et al.*, 2011 who also found little change in foliar N content with elevation in Ecuador). Although growth often appears to be N-limited (especially on landslide soil, Fetcher *et al.*, 1996), it is not clear that montane forests are N limited in general (Bruijnzeel & Proctor, 1995; Tanner *et al.*, 1998; Benner *et al.*, 2010; van de Weg *et al.*, 2009, 2012a; Lloyd *et al.*, 2010). *JULES* does include leaf N effects in its calculations of *GPP* (which assume that V_{Cmax} at 25 °C is directly proportional to canopy top-leaf N:C ratio N_{l0}, Table 1), however, between-site differences in foliar N are slight in this transect (Table 1) which is why our *JULES* results were insensitive to variation in N_{l0}. From our results, therefore, we cannot conclude that leaf N content and N limitation are important drivers of *GPP* along this transect.

Finally, it has often been noted that cloud forest leaves exhibit 'xeromorphic' features despite the generally wet conditions: leaves are generally smaller (microphylls and notophylls) with a thicker lamina, better-developed palisade tissue and thicker outer epidermal walls and cuticles and more likely to be simple (i.e. not compound) and hypostomatous (Grubb *et al.*, 1963; Grubb & Whitmore, 1966; Friend & Woodward, 1990; Bruijnzeel & Proctor, 1995; Richards *et al.*, 1996; Willmer & Fricker, 1996; Waide *et al.*, 1998). However, many so-called 'xeromorphic traits' appear rather to aid the removal of water from the leaf surface during fog than reduce water loss (Haworth & McElwain 2008). It seems logical to assume that fog and low cloud permeating the canopy depress leaf temperatures, however, UV-B radiation is proportionately higher in cloud forests because of differential transmission (Bruijnzeel & Proctor, 1995; Foster, 2001) and plants in environments with low air temperatures but high radiation loads sometimes also have architectural adaptations that allow tissue temperatures to be higher than air temperatures (see discussions in Friend & Woodward, 1990; Haworth & McElwain 2008; Landsberg & Sands, 2011). Finally, in cloud forests water films frequently form over leaf surfaces, impeding gas exchange (Richards *et al.*, 1996; Dietz *et al.*, 2007) and allowing the growth of epiphylls and eukaryotic pathogens which reduce leaf photosynthetic efficiency and shorten leaf longevity (Dietz *et al.*, 2007; Salinas *et al.*, 2011). These various 'leaf structural' effects may have a net positive or a net negative effect on cloud forest *GPP*, but in the absence of better field data we cannot be certain that their net effect is significant in this transect.

Autotrophic respiration

Our values for simulated R_a were underestimates in comparison to both measurements and the range of values suggested by Luyssaert *et al.*, (2007). Robertson *et al.*, (2010) found that stem CO_2 efflux followed a simple exponential trend with decreasing temperature in our transect (with Q_{10} value 1.5), which broadly supports the trend of our *JULES* results, although not their magnitude. Increasing the proportion of *GPP* allocated to growth r_g from its default value (0.25, Appendix S2) was the only parameter change of those tested that moved R_a closer to the measurement points, but in the absence of field values for r_g this result must be considered only suggestive (Appendix S2).

Evidence from Kosñipata suggests that the root component of R_a is fairly independent of temperature (at least, above freezing temperatures), so this temperature dependence is being driven by the aboveground components of R_a (Silva Espejo *et al.*, 2012; Huaraca Huasco *et al.*, 2012; Farfan Amezquita *et al.*, 2012). In simulating R_a, *JULES* follows a scheme more sophisticated than Q_{10} with R_a following a hump-shaped relationship with temperature based on the carboxylation rate of photosynthesis V_{Cmax} (declining both at low and at high temperatures, Cox, 2001; Clark *et al.*, 2011 and see discussions in Atkin *et al.*, 2005, 2008). Some recent research has additionally included acclimation effects in this scheme (e.g. Atkin *et al.*, 2008), but this is not yet in any official release (or in v2.2 of *JULES* used in this study).

Apart from a small number of parameters such as *LAI*, canopy height, V_{Cmax} and leaf N concentration, differences between biomes (e.g. differences in the R_a relationship) must be described in *JULES* through introducing new Plant Functional Types (PFTs) (the only default tropical forest vegetation type is 'broadleaf tree'). Many groups are working on widening the PFTs available to DGVMs (e.g. Westoby & Wright, 2006; Prentice *et al.*, 2007; Fisher *et al.*, 2010b), which is necessary in the biodiverse tropical zone where a greater proportion of species are specialists (Ghazoul & Sheil, 2010). A wider set of PFTs could greatly improve the representation of R_a in this model and in comparison to field data.

Heterotrophic respiration

Our values for simulated R_h were overestimates in comparison to both measurements and the range of values suggested by Luyssaert *et al.*, (2007) below the upper montane zone. Although it is well accepted that instantaneous within-site variations in R_h follow exponential Q_{10} functions of temperature below oxygen diffusion limitation (Robinson *et al.*, 2008), between-site differences do not appear to do so in this transect (Zimmermann *et al.*, 2009a, b Zimmermann *et al.*, 2010). Increasing the proportion of *GPP* allocated to growth r_g from its default value (0.25, Appendix S2) was the only parameter change that moved R_h closer to the measurement points, but in the absence of field values for r_g this result must be considered only suggestive (Appendix S2).

In general, heterotrophic soil respiration is controlled by substrate supply, microbial biomass and other climate factors such as precipitation in addition to temperature (Zimmermann *et al.*, 2010; also see Metcalfe *et al.*, 2007, 2011; Cornwell *et al.*, 2008; Sayer *et al.*, 2011) so these presumably become dominant at larger spatial scales and over longer timescales despite the clear temperature controls on short-term within-site responses, perhaps via plant trait interactions (Cornwell *et al.*, 2008). Soil moisture is known to explain much global between-site variation in R_h and soil mineralization rates (Robinson *et al.*, 2008; Ghazoul & Sheil, 2010) although in the Kosñipata transect it has proved challenging to distinguish temperature and moisture effects because low temperatures and reduced precipitation occur in the same season, both decreasing respiration rates (Zimmermann *et al.*, 2010). Finally, note that Zimmermann *et al.*, (2010) found little change in soil respiration with elevation in this transect, so if processes of decomposition and N mineralization per unit mass decrease in the upper montane zone, as implied by the leaf N values at Wayqecha (see above), then, from the results of a leaf and wood translocation experiment (Salinas *et al.*, 2011), either the mass of organic material builds up to compensate (to yield a similar flux per unit area) or more complicated effects such as soil priming must be occurring (Sayer *et al.*, 2011).

Net primary productivity

Our values for simulated *NPP* were overestimates in comparison to both measurements and the range of values suggested by Clark *et al.*, (2001b) and Luyssaert *et al.*, (2007) below the upper montane zone. Because *NEP* is close to zero for all our sites, long-term mean *NPP* aligns very closely to R_h as is to be expected under equilibrium conditions. As with *GPP*, there is much debate over the mechanisms through which *NPP* varies between biomes (e.g. Malhi *et al.*, 2009; Metcalfe *et al.*, 2009; Aragão *et al.*, 2009; Girardin *et al.*, 2010; see also the *NPP* databases of Scurlock & Olson, 2002; Malhi *et al.*, 2011). Here, however, because of the mechanistic approach of *JULES* (in common with all DGVMs) *GPP* and R_a are modelled explicitly and separately and then *NPP* is calculated as the difference (GPP–R_a) (Table 2), so the controlling factors of *NPP* have already been discussed above as controls either on *GPP* or on R_a.

Increasing the proportion of *GPP* allocated to growth r_g from its default value (0.25, Appendix S2) was the only parameter change that moved *NPP* closer to the measurement points, but in the absence of field values for r_g this result must be considered only suggestive (Appendix S2). However, note that this simple change simultaneously improved the representation of simulated R_a, R_h and *NPP* in *JULES*.

Net ecosystem productivity

The Joint UK Land Environment Simulator, *JULES* predicts all the study sites to be weak carbon sinks (i.e. car-

bon is being sequestered in all ecosystems along this transect) and the magnitude of these sinks is only a little below the suggested values of Luyssaert et al., (2007) and Malhi (2010). Increasing the proportion of GPP allocated to growth r_g from its default value (0.25, Appendix S2) tended to decrease NEP at all sites but not change its sign (as a consequence of increased growth and/or maintenance respiration, see Appendix S2). Note that because JULES assumes a mass balance under equilibrium conditions: all these nonzero carbon budgets are caused by transient effects (e.g. from successional dynamics, climate variability or the changes in atmospheric CO_2 concentration since ca. 1850, Intergovernmental Panel on Climate Change, 2007).

Carbon use efficiency

The phrase 'carbon use efficiency' is misleading at the ecosystem level and it should not be understood that tropical forests are 'less efficient' than their temperate counterparts: overall, they simply appear to allocate proportionately fewer carbon resources to growth (the same argument applies to similar terms such as 'biomass production efficiency', Vicca et al., 2012). Low CUE may not indicate inefficiency: for example, high respiration may be a necessary consequence of the elevated metabolic rates necessary for photosynthesis in highly variable light environments (Huaraca Huasco et al., 2012 found a depressed value for CUE in the transition zone to permanent cloud in our transect, perhaps showing this respiration effect).

The Joint UK Land Environment Simulator, JULES predicts CUE values at all sites close to 0.5, clearly higher than measured values (Fig. 2). However, in answer to our third research question, JULES does not return the increase of CUE with elevation suggested by Zhang et al., (2009) and Piao et al., (2010). Atkin et al., (2005) and Zhang et al., (2009) found evidence for temperature-mediated differences in CUE and Piao et al., (2010) suggested a parabolic relationship between CUE and mean annual temperature. Similarly, from a compilation of global trait, biomass and growth data, Enquist et al., (2007) found that plant CUE increased with elevation from ~0.30 at sea level to >0.60 above 1000 m asl, which implies a direct or indirect correlation with air temperature. However, neither available measurements nor our simulations with JULES support this theory in this particular elevational transect.

Modelled CUE follows a daily cycle, increasing as GPP declines (and becoming undefined at night), but what about seasonal change? Monteith (1981) assumed minimal change within the growing season (over time periods of at least a few weeks) but CUE is also known to depend on successional stage (Mäkelä & Valentine,

2001; Malhi et al., 2009; Landsberg & Sands, 2011) indicating that CUE depends not only on growth rates but also on whether high growth is caused by seasonality and mobilization of stored resources (change in growth/maintenance allocation, Appendix S2) or inherent to a particular plant functional group (e.g. pioneers). Recent evidence suggests that CUE does follow an annual cycle at some sites, with storage of carbon during one season as a buffer against another season (Malhi et al., 1999; Farfan Amezquita et al., 2012; Huaraca Huasco et al., 2012; Silva Espejo et al., 2012), however, simulations currently do not capture these effects.

Chambers et al., (2004) suggested that in nutrient-deficient forests such as central Amazon terra firme, more carbon is fixed via photosynthesis than can be utilized by growth and functional respiration, pointing to an edaphic rather than biotic control (e.g. nutrient or moisture limitation) and this perspective is also supported by more recent evidence (Malhi et al., 2009; Aragão et al., 2009; cf. similar mechanisms reviewed by Lloyd et al., 2010; Vicca et al., 2012). CUE may also be controlled by plant traits (Enquist et al., 2007) which may of course themselves be controlled by climate-related and edaphic factors. The model FUN, for example, includes a mechanism whereby plants preferentially devote resources (GPP) to N acquisition before growth (NPP) with the effect that greater N acquisition costs will directly reduce both productivity and CUE (Fisher et al., 2010a). This mechanism suggests a reduction in CUE in N limited ecosystems, e.g. the upper montane zone of this transect. Although our simulations are supported by this trend, this may be coincidental because JULES does not include such N allocation routines (Clark et al., 2011).

Increasing the proportion of GPP allocated to growth r_g from its default value (0.25, Appendix S2) simultaneously improved the fit between simulated R_a, R_h and NPP and available measurements (see above), and, to a lesser extent, CUE. However, what is the correct value? Combining the relationship between r_g (the fraction of carbon allocated to growth), CUE and γ (ratio of growth to maintenance respiration) (Appendix S2): $r_g = \frac{\gamma(1-CUE)}{\gamma+CUE}$ with the respiration measurements of Robertson et al., (2010) for this transect (Appendix S2) suggests that r_g=0.33 is a more reasonable value in lowland forest at Caxiuanã (using measured CUE = 0.33, Table 2, γ=0.32) and in upper montane forests a lower value for r_g should be appropriate, perhaps as low as 0.05 at Wayqecha (using CUE = 0.33, Table 2, γ=0.03).

If CUE does not vary greatly with elevation then changes in r_g must be controlled by γ, which is at least partly controlled by pressure (Gale, 1972; Friend & Woodward, 1990; Raich et al., 2006). Moving from

Caxiuanã to Wayqecha, mean annual temperature drops from 26.2 to 12.5 °C (Table 2) and total atmospheric pressure from 1023 to 706 hPa (measured annual mean). Therefore, the mean equilibrium solubility of oxygen decreases from 8.6 to 7.7 mg O_2 L^{-1} (Henry's Law, Appendix S3; equivalent to 0.82% v/v O_2 in aqueous solution). Lower dissolved oxygen might impose a constraint on R_a and its components R_g and R_m (e.g. Guo *et al.*, 2008), especially in environments where irradiance (and therefore photosynthesis) is intermittent so respiration is more likely to temporarily deplete reserves of O_2 held inside leaf cells (Öpik, 1980) and the slow rate of diffusion of O_2 both within cells and across leaf boundary layers will hamper replenishment from the atmosphere and may induce anaerobic respiration (fermentation). Reduced partial pressure of CO_2 can reduce photosynthesis, although this is partially offset by increased diffusivity of CO_2 and reduced photorespiration in C_3 plants (Bowman *et al.*, 1999; Raich *et al.*, 2006). Metabolically important thresholds for tropical montane vegetation are not well known (Friend & Woodward, 1990), but dissolved oxygen concentrations below 4 mg L^{-1} are generally accepted to mean 'only a few kinds of fish and insects can survive' in rivers in the United States (Behar, 1997) and Carrera-Burneo & Gunkel (2003) suggested that 5 mg O_2 L^{-1} was restrictive to ecosystem function in the Ecuadorean Andes. Equating the health thresholds of water courses to thresholds for cloud forest vegetation is speculative, but it seems reasonable to suggest that low pressure (Gale, 1972; Iwabuchi *et al.*, 1995; Bowman *et al.*, 1999; Guo *et al.*, 2008) may be causing some level of stress in cloud forest vegetation in addition to low temperature effects. Reduced diffusive and photosynthetic rates as a consequence of reduced atmospheric partial pressures would have a significant effect on the productivity and carbon balance of tropical montane forests (Friend & Woodward, 1990; Körner, 1998).

In this study we have applied the vegetation model *JULES* at six tropical sites, making use of an elevational transect in the Peruvian Andes (Malhi *et al.*, 2010) and data from *RAINFOR* sites across the lowland Amazon basin. Field-based estimation of respiration and productivity in tropical forests is challenging work and very few sites have been intensively monitored with all components of the forest carbon cycle measured *in situ* (Metcalfe *et al.*, 2009; Malhi *et al.*, 2009). The need for good model simulations to fill the gaps between well studied tropical forests is well-known and we present robust predictions of all ecosystem-level carbon fluxes, forming a uniquely detailed picture of carbon cycling across a wide range of neotropical forests.

Simulated forest ecosystem carbon fluxes showed generally close agreement with measurements from lowland and lower montane forests, although not upper montane forests where simulated vegetation died back. From a review of the dominant mechanisms influencing the carbon budget and how its components vary with elevation, temperature and pressure, we conclude that carbon use efficiency in this transect does not increase with elevation as has been found in other studies (Zhang *et al.*, 2009; Piao *et al.*, 2010; but see Zach *et al.*, 2010). The carbon efficiency of forests under different temperature regimes has recently received much attention and we develop this viewpoint to suggest that the allocation of carbon to growth and maintenance within the vegetation canopy is also important. Our simulations indicate that better estimates of these parameters will improve the ability of *JULES* to simulate forest carbon cycle components. The variation of all these quantities with elevation has important implications for theories on carbon flows through tropical forests and, therefore, for carbon budget and forest productivity assessment not only in the Andes-Amazon region but across all tropical zones.

Acknowledgements

References

Alton P, Mercado L, North P (2007) A sensitivity analysis of the land-surface scheme JULES conducted for three forest biomes: biophysical parameters, model processes, and meteorological driving data. *Global Biogeochemical Cycles*, **20**, GB1008.

Amorim Costa J (2005) Análises físicas e fertilidade em solos de terra preta e latossolo amarelo sob florestas na região de Caxiuanã, Pa. *Relatório Final*, Museu Paraense Emílio Goeldi, Brazil.

Anderson LO, Malhi Y, Ladle RJ *et al.* (2009) Influence of landscape heterogeneity on spatial patterns of wood productivity, wood specific density and above ground biomass in Amazonia. *Biogeosciences Discussions*, **6**, 2039–2083.

Aragão LEOC, Malhi Y, Metcalfe DB *et al.* (2009) Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils. *Biogeosciences*, **6**, 2759–2778.

Araújo AC, Nobre AD, Kruijt B *et al.* (2002) Comparative measurements of carbon dioxide fluxes from two nearby towers in a central Amazonian rainforest: the Manaus LBA site. *Journal of Geophysical Research D*, **107**(D20), 8090(LBA58).

Ashton PS (2003) Floristic zonation of tree communities on wet tropical mountains revisited. *Perspectives in Plant Ecology, Evolution and Systematics*, **6**, 87–104.

Atkin OK, Bruhn D, Hurry VW, Tjoelker MG (2005) The hot and the cold: unravelling the variable response of plant respiration to temperature. *Functional Plant Biology*, **32**, 87–105.

Atkin OK, Atkinson LJ, Fisher RA *et al.* (2008) Using temperature-dependent changes in leaf scaling relationships to quantitatively account for thermal acclimation of respiration in a coupled global climate–vegetation model. *Global Change Biology*, **14**, 2709–2726.

Avissar R, Nobre CA (2002) Preface to special issue on the Large-Scale Biosphere-Atmosphere experiment in Amazonia (LBA). *Journal of Geophysical Research D*, **107** (D20), 8034(LBA1).

Behar S (1997) Testing the Waters: Chemical & Physical Vital Signs of a River. *Manual*, River Watch Network, Dubuque, Iowa.

Benner J, Vitousek PM, Ostertag R (2010). Nutrient cycling and nutrient limitation in tropical montane cloud forests. In: *Tropical Montane Cloud Forests* (eds Bruijnzeel LA, Scatena FN, Hamilton LS), pp. 90–100. CUP, Cambridge, UK.

Best MJ, Pryor M, Clark DB *et al.* (2011) The Joint UK Land Environment Simulator (JULES), model description – Part 1: energy and water fluxes. *Geoscientific Model Development*, **4**, 677–699.

Bonan G (2008) *Ecological Climatology* (2nd edn). CUP, Cambridge, UK.

Bowman WD, Keller A, Nelson M (1999) Altitudinal variation in leaf gas exchange, nitrogen and phosphorus concentrations, and leaf mass per area in populations of *Frasera speciosa*. *Arctic, Antarctic, and Alpine Research*, **31**, 191–195.

Bruijnzeel LA, Proctor J (1995) Hydrology and biogeochemistry of tropical montane cloud forests: what do we really know? In: *Tropical Montane Cloud Forests* (eds Hamilton LS, Juvik JO, Scatena FN), pp. 38–78. Springer-Verlag, New York.

Butt N, Malhi Y, Phillips O, New M (2008) Floristic and functional affiliations of woody plants with climate in western Amazonia. *Journal of Biogeography*, **35**, 939–950.

Carrera-Burneo P, Gunkel G (2003) Ecology of a high Andean stream, Rio Itambi, Otavalo, Ecuador. *Limnologica*, **33**, 29–43.

Chambers JQ, dos Santos J, Ribeiro RJ, Higuchi N (2001) Tree damage, allometric relationships, and above-ground net primary production in central Amazon forest. *Forest Ecology and Management*, **152**, 73–84.

Chambers JQ, Tribuzy ES, Toledo LC *et al.* (2004) Respiration from a tropical forest ecosystem: partitioning of sources and low carbon use efficiency. *Ecological Applications*, **14** (suppl.), S72–S88.

Chapin FS, Matson P, Mooney HA (2002) *Principles of Terrestrial Ecosystem Ecology*. Springer, New York.

Clark DA (2004) Sources or sinks? The responses of tropical forests to current and future climate and atmospheric composition. *Philosophical Transactions of the Royal Society of London B*, **359**, 477–491.

Clark DA, Brown S, Kicklighter DW, Chambers JQ, Thomlinson JR, Ni J (2001a) Measuring net primary production in forests: concepts and field methods. *Ecological Applications*, **11**, 356–370.

Clark DA, Brown S, Kicklighter DW, Chambers JQ, Thomlinson JR, Ni J, Holland EA (2001b) Net primary production in tropical forests: an evaluation and synthesis of existing field data. *Ecological Applications*, **11**, 371–384.

Clark DB, Mercado LM, Sitch S *et al.* (2011) The Joint UK Land Environment Simulator (JULES), model description – Part 2: carbon fluxes and vegetation dynamics. *Geoscientific Model Development*, **4**, 701–722.

Cornwell WK, Cornelissen JHC, Amatangelo K *et al.* (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters*, **11**, 1065–1071.

Cosby BJ, Hornberger GM, Clapp RB, Ginn TR (1984) A statistical exploration of the relationships of soil moisture characteristics to the physical properties of soils. *Water Resources Research*, **20**, 682–690.

Cox PM (2001) Description of the "TRIFFID" dynamic global vegetation model. *Hadley Centre Technical Note*, **24**, 1–16.

Dharssi I, Vidale PL, Verhoef A, Macpherson B, Jones C, Best M (2009) New soil physical properties implemented in the Unified Model at PS18. *Met Office Technical Report*, **528**, 1–33.

Dietz J, Leuschner C, Hölscher D, Kreilein H (2007) Vertical patterns and duration of surface wetness in an old-growth tropical montane forest, Indonesia. *Flora*, **202**, 111–117.

Enquist BJ, Kerkhoff AJ, Stark SC, Swenson NG, McCarthy MC, Price CA (2007) A general integrative model for scaling plant growth, carbon flux, and functional trait spectra. *Nature*, **449**, 218–222.

Eva HD, Huber O, Achard F *et al.* (2005) A proposal for defining the geographical boundaries of Amazonia. *Report*, European Communities, Luxembourg.

Farfan Amezquita F, Doughty CE, Silva Espejo JE *et al.* (submitted 2012) The productivity, metabolism and carbon cycle of two lowland tropical forest plots in SW Amazonia, Peru. *Plant Ecology & Diversity*.

Fetcher N, Haines BL, Cordero RA, Lodge DJ, Walker LR, Fernández DS, Lawrence WT (1996) Responses of tropical plants to nutrients and light on a landslide in Puerto Rico. *Journal of Ecology*, **84**, 331–341.

Fisher RA, Williams M, Ruivo MDL, de Costa AL, Meir P (2008) Evaluating climatic and soil water controls on evapotranspiration at two Amazonian rainforest sites. *Agricultural and Forest Meteorology*, **148**, 850–861.

Fisher JB, Sitch S, Malhi Y, Fisher RA, Huntingford C, Tan SY (2010a) Carbon cost of plant nitrogen acquisition: a mechanistic, globally applicable model of plant nitrogen uptake, retranslocation, and fixation. *Global Biogeochemical Cycles*, **24**, GB1014.

Fisher R, McDowell N, Purves D *et al.* (2010b) Assessing uncertainties in a second-generation dynamic vegetation model caused by ecological scale limitations. *New Phytologist*, **187**, 666–681.

Fisher JB, Malhi Y, Torres IC *et al.* (2011) Nutrient limitation in rainforests and cloud forests along a 3000 m elevation gradient in the Peruvian Andes. *Oecologia* (in review).

Foster P (2001) The potential negative impacts of global climate change on tropical montane cloud forests. *Earth-Science Reviews*, **55**, 73–106.

Friend AD, Woodward FI (1990) Evolutionary and ecophysiological responses of mountain plants to the growing season environment. *Advances in Ecological Research*, **20**, 59–124.

Fyllas NM, Patiño S, Baker TR *et al.* (2009) Basin-wide variations in foliar properties of Amazonian forest: phylogeny, soils and climate. *Biogeosciences*, **6**, 2677–2708.

Gale J (1972) Availability of carbon dioxide for photosynthesis at high altitudes: theoretical considerations. *Ecology*, **53**, 494–497.

Ghazoul J, Sheil D (2010) *Tropical Rain Forest Ecology, Diversity, and Conservation*. OUP, Oxford, UK.

Girardin CAJ, Malhi Y, Aragão LEOC *et al.* (2010) Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes. *Global Change Biology*, **16**, 3176–3192.

Graham EA, Mulkey SS, Kitajima K, Phillips NG, Wright SJ (2003) Cloud cover limits net CO_2 uptake and growth of a rainforest tree during tropical rainy seasons. *Proceedings of the National Academy of Sciences USA*, **100**, 572–576.

Grubb PJ, Whitmore TC (1966) A comparison of montane and lowland rain forest in Ecuador II The climate and its effects on the distribution and physiognomy of the forests.. *Journal of Ecology*, **54**, 303–333.

Grubb PJ, Lloyd JR, Pennington TD, Whitmore TC (1963) A comparison of montane and lowland rain forest in Ecuador I The forest structure, physiognomy, and floristics.. *Journal of Ecology*, **51**, 567–601.

Guo S, Tang Y, Gao F, Ai W, Qin L (2008) Effects of low pressure and hypoxia on growth and development of wheat. *Acta Astronautica*, **63**, 1081–1085.

Haworth M, McElwain J (2008) Hot, dry, wet, cold or toxic? Revisiting the ecological significance of leaf and cuticular micromorphology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **262**, 79–90.

Hodnett MG, Tomasella J (2002) Marked differences between van Genuchten soil water-retention parameters for temperate and tropical soils: a new water-retention pedo-transfer functions developed for tropical soils. *Geoderma*, **108**, 155–180.

Houghton RA, Gloor M, Lloyd J, Potter C (2009). The regional carbon budget. In: *Amazonia and Global Change* (eds Keller M, Bustamante M, Gash J, Silva Dias P), pp. 409–428. American Geophysical Union, Washington, DC.

Huaraca Huasco W, Girardin CAJ, Doughty CE *et al.* (submitted 2012) Seasonal production, allocation and cycling of carbon in two mid-elevation tropical montane forest plots in the Peruvian Andes. *Plant Ecology & Diversity*, (in review).

Intergovernmental Panel on Climate Change (2007) Climate Change 2007: the Fourth IPCC Assessment Report. CUP, Cambridge, UK.

Iwabuchi K, Goto E, Takakura T (1995) Effect of O_2 pressure under low air pressure on net photosynthetic rate of spinach. *Acta Horticulturae*, **399**, 101–106.

Iwata H, Malhi Y, von Randow C (2005) Gap-filling measurements of carbon dioxide storage in tropical rainforest canopy airspace. *Agricultural and Forest Meteorology*, **132**, 305–314.

Kira T (1978). Community architecture and organic matter dynamics in tropical lowland rain forests of Southeast Asia with special reference to Pasoh Forest, West Malaysia. In: *Tropical Trees as Living Systems* (eds Tomlinson PB, Zimmerman MH), pp. 561–590. CUP, Cambridge, UK.

Körner C (1998) A re-assessment of high elevation treeline positions and their explanation. *Oecologia*, **115**, 445–459.

Landsberg J, Sands P (2011) *Physiological Ecology of Forest Production*. Academic Press, Amsterdam, The Netherlands.

Landsberg J, Waring RH (2004) Top-down models and flux measurements are complementary methods of estimating carbon sequestration by forests: illustrations using the 3-PG model. In: *Forests at the Land-Atmosphere Interface* (eds Mencuccini M, Grace J, Moncrieff J, McNaughton KG), pp. 37–50. CABI Publishing, Wallingford, UK.

Lewis SL, Lloyd J, Sitch S, Mitchard ETA, Laurance WF (2009) Changing Ecology of Tropical Forests: evidence and Drivers. *Annual Review of Ecology, Evolution and Systematics*, **40**, 529–549.

Lisboa PLB (1997). A Estação Científica Ferreira Penna/ECFPn. In: *Caxiuanã* (ed. Lisboa PLB), pp. 20–49. Museu Paraense Emílio Goeldi, Belém, Brazil.

Lloyd J, Patiño S, Paiva RQ *et al.* (2010) Optimisation of photosynthetic carbon gain and within-canopy gradients of associated foliar traits for Amazon forest trees. *Biogeosciences*, **7**, 1833–1859.

Lovett GM, Cole JJ, Pace ML (2006) Is net ecosystem production equal to ecosystem carbon accumulation? *Ecosystems*, **9**, 1–4.

Luyssaert S, Inglima I, Jung M *et al.* (2007) CO$_2$ balance of boreal, temperate, and tropical forests derived from a global database. *Global Change Biology*, **13**, 2509–2537.

Luyssaert S, Schulze E, Börner A *et al.* (2008) Old-growth forests as global carbon sinks. *Nature*, **455**, 213–215.

Mäkelä A, Valentine HT (2001) The ratio of NPP to GPP: evidence of change over the course of stand development. *Tree Physiology*, **21**, 1015–1030.

Malhi Y (2010) The carbon balance of tropical forest regions, 1990-2005. *Current Opinion in Environmental Sustainability*, **2**, 237–244.

Malhi Y (2012) The productivity, metabolism and carbon cycle of tropical forest vegetation. *Journal of Ecology*, **100**, 65–75.

Malhi Y, Grace J (2000) Tropical forests and atmospheric carbon dioxide. *Tree*, **15**, 332–337.

Malhi Y, Baldocchi DD, Jarvis PG (1999) The carbon balance of tropical, temperate and boreal forests. *Plant, Cell and Environment*, **22**, 715–740.

Malhi Y, Pegoraro E, Nobre AD, Pereira MGP, Grace J, Culf AD, Clement R (2002) Energy and water dynamics of a central Amazonian rain forest. *Journal of Geophysical Research*, **107**(D20), LBA45.

Malhi Y, Aragão LEOC, Metcalfe DB *et al.* (2009) Comprehensive assessment of carbon productivity, allocation and storage in three Amazonian forests. *Global Change Biology*, **15**, 1255–1274.

Malhi Y, Silman M, Salinas N, Bush M, Meir P, Saatchi S (2010) Introduction: elevation gradients in the tropics: laboratories for ecosystem ecology and global change research. *Global Change Biology*, **16**, 3171–3175.

Malhi Y, Doughty C, Galbraith D (2011) The allocation of ecosystem net primary productivity in tropical forests. *Philosophical Transactions of the Royal Society B*, **366**, 3225–3245.

Marthews TR, Burslem DFRP, Paton SR, Yangüez F, Mullins CE (2008) Soil drying in a tropical forest: three distinct environments controlled by gap size. *Ecological Modelling*, **216**, 369–384.

Marthews TR, Malhi Y, Iwata H (2012) Calculating downward longwave radiation under clear and cloudy conditions over a tropical lowland forest site: an evaluation of model schemes for hourly data. *Theoretical and Applied Climatology*, **107**, 461–477.

Mercado L, Lloyd J, Carswell F, Malhi Y, Meir P, Nobre AD (2006) Modelling Amazonian forest eddy covariance data: a comparison of big leaf versus sun/shade models for the C-14 tower at Manaus I. *Canopy photosynthesis. Acta Amazonica*, **36**, 69–82.

Mercado LM, Huntingford C, Gash JHC, Cox PM, Jogireddy V (2007) Improving the representation of radiation interception and photosynthesis for climate model applications. *Tellus B*, **59**, 553–565.

Mercado L, Lloyd J, Dolman AJ, Sitch S, Patiño S (2009) Modelling basin-wide variations in Amazon forest productivity – Part 1: model calibration, evaluation and upscaling functions for canopy photosynthesis. *Biogeosciences*, **6**, 1247–1272.

Mercado LM, Patiño S, Domingues TF *et al.* (2011) Variations in Amazon forest productivity correlated with foliar nutrients and modelled rates of photosynthetic carbon supply. *Philosophical Transactions of the Royal Society B*, **366**, 3316–3329.

Metcalfe DB, Meir P, Aragão LEOC *et al.* (2007) Factors controlling spatio-temporal variation in carbon dioxide efflux from surface litter, roots, and soil organic matter at four rain forest sites in the eastern Amazon. *Journal of Geophysical Research G*, **112**, G04001.

Metcalfe D, Phillips O, Baker T *et al.* (2009) Measuring Tropical Forest Carbon Allocation And Cycling. *RAINFOR* Field Manual. Available at: http://www.geog.leeds.ac.uk/projects/rainfor/pages/manuals_eng.html (accessed 14 May 2012).

Metcalfe DB, Meir P, Aragão LEOC *et al.* (2010) Shifts in plant respiration and carbon use efficiency at a large-scale drought experiment in the eastern Amazon. *New Phytologist*, **187**, 608–621.

Metcalfe DB, Fisher RA, Wardle DA (2011) Plant communities as drivers of soil respiration: pathways, mechanisms, and significance for global change. *Biogeosciences*, **8**, 2047–2061.

Monteith JL (1981) Climatic variation and the growth of crops. *Quarterly Journal of the Royal Meteorological Society*, **107**, 749–774.

Moser G, Leuschner C, Hertel D, Graefe S, Iost S (2011) Elevation effects on the carbon budget of tropical mountain forests (S Ecuador): the role of the belowground compartment. *Global Change Biology*, **17**, 2211–2226.

van Oijen M, Schapendonk A, Höglind M (2010) On the relative magnitudes of photosynthesis, respiration, growth and carbon storage in vegetation. *Annals of Botany*, **105**, 793–797.

Öpik H (1980) *The Respiration of Higher Plants*. Edward Arnold, London, UK.

Pan Y, Birdsey RA, Fang J *et al.* (2011) A large and persistent carbon sink in the world's forests. *Science*, **333**, 988–993.

Park S, Jiménez R, Daube BC *et al.* (2007) The CO$_2$ tracer clock for the tropical tropopause layer. *Atmospheric Chemistry and Physics*, **7**, 3989–4000.

Patiño S, Lloyd J, Paiva R *et al.* (2009) Branch xylem density variations across the Amazon Basin. *Biogeosciences*, **6**, 545–568.

Pennington TD, Reynel C, Daza A (2004) *Illustrated guide to the Trees of Peru*. David Hunt, Sherborne, UK.

Phillips OL, Aragão LEOC, Lewis SL *et al.* (2009) Drought Sensitivity of the Amazon Rainforest. *Science*, **323**, 1344–1347.

Piao S, Luyssaert S, Ciais P *et al.* (2010) Forest annual carbon cost: a global-scale analysis of autotrophic respiration. *Ecology*, **91**, 652–661.

Pires JM, Prance GT (1985) The vegetation types of the brazilian amazon. In: *Amazonia* (eds Prance GT, Lovejoy TE), pp. 109–145. Pergamon Press, Oxford, UK.

Prentice IC, Bondeau A, Cramer W *et al.* (2007). Dynamic global vegetation modeling: quantifying terrestrial ecosystem responses to large-scale environmental change. In: *Terrestrial Ecosystems in a Changing World* (eds Canadell JG, Pataki DE, Pitelka LF), pp. 175–192. Springer, Berlin, Germany.

Quesada CA (2008) Soil vegetation interactions across Amazonia. PhD thesis, University of Leeds, UK.

Quesada CA, Lloyd J, Schwarz M *et al.* (2010) Variations in chemical and physical properties of Amazon forest soils in relation to their genesis. *Biogeosciences*, **7**, 1515–1541.

R Development Core Team (2011) *R: A language and environment for statistical computing, version 2.13.1*. R Foundation for Statistical Computing, Vienna. Available at: http://www.R-project.org (accessed 14 May 2012).

Raich JW, Russell AE, Kitayama K, Parton WJ, Vitousek PM (2006) Temperature influences carbon accumulation in moist tropical forests. *Ecology*, **87**, 76–87.

Richards PW, Walsh RPD, Baillie IC, Greig-Smith P (1996) *The Tropical Rain Forest* (2nd ed). CUP, Cambridge, UK.

Robertson AL, Malhi Y, Farfan-Amezquita F, Aragão LEOC, Silva Espejo JE, Robertson MA (2010) Stem respiration in tropical forests along an elevation gradient in the Amazon and Andes. *Global Change Biology*, **16**, 3193–3204.

Robinson DA, Campbell CS, Hopmans JW *et al.* (2008) Soil Moisture Measurement for Ecological and Hydrological Watershed-Scale Observatories: a Review. *Vadose Zone Journal*, **7**, 358–389.

Salinas N, Malhi Y, Meir P *et al.* (2011) The sensitivity of tropical leaf litter decomposition to temperature: results from a large-scale leaf translocation experiment along an elevation gradient in Peruvian forests. *New Phytologist*, **189**, 967–977.

Sayer EJ, Heard MS, Grant HK, Marthews TR, Tanner EVJ (2011) Soil carbon release enhanced by increased tropical forest litterfall. *Nature Climate Change*, **1**, 304–307.

Scurlock JMO, Olson RJ (2002) Terrestrial net primary productivity — A brief history and a new worldwide database. *Environmental Reviews*, **10**, 91–109.

Silva Espejo JE, Girardin CAJ, Doughty C *et al.* (submitted 2012) Productivity and carbon allocation in a high elevation Tropical mountain cloud forest of the peruvian Andes. *Plant Ecology & Diversity*, (in review).

ter Steege H, Pitman N, Sabatier D *et al.* (2003) A spatial model of tree α-diversity and tree density for the Amazon. *Biodiversity and Conservation*, **12**, 2255–2277.

Tanner EVJ, Vitousek PM, Cuevas E (1998) Experimental investigation of nutrient limitation of forest growth on wet tropical mountains. *Ecology*, **79**, 10–22.

Terborgh J, Andresen E (1998) The composition of Amazonian forests: patterns at local and regional scales. *Journal of Tropical Ecology*, **14**, 645–664.

Vicca S, Luyssaert S, Peñuelas J *et al.* (2012) Fertile forests produce biomass more efficiently. *Ecology Letters*, **15**, 520–526.

Waide RB, Zimmerman JK, Scatena FN (1998) Controls of primary productivity: lessons from the Luquillo Mountains in Puerto Rico. *Ecology*, **79**, 31–37.

Walsh RPD (1996). Microclimate and hydrology. In: *The Tropical Rain Forest* 2nd ed (eds Richards PW, Walsh RPD, Baillie IC, Greig-Smith P), pp. 206–236,503–540. CUP, Cambridge, UK.

van de Weg MJ, Meir P, Grace J, Atkin OK (2009) Altitudinal variation in leaf mass per unit area, leaf tissue density and foliar nitrogen and phosphorus content along an Amazon-Andes gradient in Peru. *Plant Ecology and Diversity*, **2**, 243–254.

van de Weg MJ, Meir P, Grace J, Ramos GD (2012a) Photosynthetic parameters, dark respiration and leaf traits in the canopy of a Peruvian tropical montane cloud forest. *Oecologia*, **168**, 23–34.

van de Weg MJ, Meir P, Williams M, Malhi Y, Silva-Espejo J, Grace J (in review 2012b) Modelling the gross primary productivity of a high elevation tropical montane cloud forest. *Ecology*.

Westoby M, Wright IJ (2006) Land-plant ecology on the basis of functional traits. *Tree*, **21**, 261–268.

Willmer C, Fricker M (1996) *Stomata* (2nd ed). Chapman Hall, London, UK.

Yang Y, Luo Y, Finzi AC (2011) Carbon and nitrogen dynamics during forest stand development: a global synthesis. *New Phytologist*, **190**, 977–989.

Zach A, Horna V, Leuschner C, Zimmermann R (2010) Patterns of wood carbon dioxide efflux across a 2,000-m elevation transect in an Andean moist forest. *Oecologia*, **162**, 127–137.

Zhang Y, Xu M, Chen H, Adams J (2009) Global pattern of NPP to GPP ratio derived from MODIS data: effects of ecosystem type, geographical location and climate. *Global Ecology and Biogeography*, **18**, 280–290.

Zimmermann M, Meir P, Bird MI, Malhi Y, Ccahuana AJQ (2009a) Climate dependence of heterotrophic soil respiration from a soil-translocation experiment along a 3000 m tropical forest altitudinal gradient. *European Journal of Soil Science*, **60**, 895–906.

Zimmermann M, Meir P, Bird MI, Malhi Y, Ccahuana AJQ (2009b) Litter contribution to diurnal and annual soil respiration in a tropical montane cloud forest. *Soil Biology and Biochemistry*, **41**, 1338–1340.

Zimmermann M, Meir P, Bird MI, Malhi Y, Ccahuana AJQ (2010) Temporal variation and climate dependence of soil respiration and its components along a 3000 m altitudinal tropical forest gradient. *Global Biogeochemical Cycles*, **24**, GB4012.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1: Meteorological data and gap-filling (filling missing time periods and missing variables).
Appendix S2: Growth and maintenance respiration.
Appendix S3: Henry's law.
Figure S1. The theoretical variation of r_g with *CUE* and for example values of Y_g and α (see text for definitions). Uncertainty in the value of Y_g does affect r_g (lines show values at Y_g=0.75 and grey bands show values for the range $0.7 < Y_g < 0.8$), with higher values of Y_g giving lower values of r_g. The arrow shows the theoretical direction of forest succession (Landsberg & Sands, 2011 suggested that *CUE* decreases from ≈ 0.5 in young to ≈ 0.3 in mature forests, and this may be combined with an increase in carbon storage from $\alpha \approx 0$ in early successional stages to $\alpha \approx CUE$ in mature patches to give r_g decreasing from 0.25 to 0). The r_g=0.25 estmate of *JULES* (Cox, 2001; Clark *et al.*, 2011) may be understood as a maximal value for vegetation with negligible storage (high growth), *CUE* < 0.6 and Y_g=0.75.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.